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Horst R. Thieme: Mathematics in Population Biology

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Chapter One

Some General Remarks on Mathematical Modeling

ἐκ μέρους γὰρ γινώσκομεν

St Paul, 1st letter to the Corinthians, 13:9

Modeling is an attempt to see the wood for the trees. A model is a simplification or abstraction of reality (whatever that is), separating the important from the irrelevant. Actually, modeling is a part of our existence. If we want to be philosophical, we could say that we do not perceive reality as it is, but only realize a model our mind has designed from sensory stimuli and their interpretation. It seems that certain animal species perceive different models of reality which, compared to ours, are based more on hearing and smell than on sight. Many philosophers have had much deeper thoughts on this problem than I present here; following Plato's famous allegory of the cave we may say that we only see the shadows of reality, or, following Kant, that we see the phenomena rather than the noumena. St Paul (1st letter to the Corinthians, 13:9), puts it this way: *We obtain our knowledge in parts, and we prophesy in parts.* St Paul, of course, had a broader and deeper reality in mind than we are concerned with here, but if we apply his statement to a more restricted reality, we may (rather freely) paraphrase it as follows: *We obtain our knowledge from models, and we make our predictions on the basis of models.*

Since, in a wide sense, we are modeling anyway, modeling in the strict sense is the purposeful attempt to replace one model (the so-called "real world," which we typically accept without questioning) by another, deliberate, model which may give us more insight. Essentially, there seem to be two incentives for doing so: either the "real-world" model is too complex to obtain the desired insight and so is replaced by a simpler or more abstract one. Or the "real-world" model does not allow certain experiments for ethical, practical or other reasons and is replaced by a model in which all kinds of changes can be readily made and their consequences studied without causing harm.

The word *model* presumably traces back to the Latin word *modulus*, which means "little measure" (Merriam-Webster, 1994), alluding to a small-scale physical representation of a large object (e.g., a model airplane).

Mathematical modeling uses symbolic rather than physical representations, unleashing the power of mathematical analysis to increase scientific understanding. It can conveniently be divided into three stages (cf. Lin, Segel, 1974, 1988).

- (i) *Model formulation*: the translation of the scientific problem into mathematical terms.
- (ii) *Model analysis*: the mathematical solution of the model thus created.
- (iii) *Model interpretation and verification*: the interpretation of the solution and its empirical verification in terms of the original problem.

All three steps are important and useful. Already the first step—model formulation—can lead to considerable insight. For building a mathematical model, one needs clear-cut assumptions about the operating mechanisms, and it often turns out to be an unpleasant surprise that the old model—the “real world”—is far less understood than one thought. In many cases the modeling procedure—at least if one chooses parameters that are meaningful—already teaches what further knowledge is needed in order to apply the mathematical model successfully; the model analysis and its interpretation help to determine to what extent and precision new information and new data have to be collected.

Analytic and numerical tools allow the extrapolation of present states of the mathematical model into the future and, sometimes, into the past. Assumptions, initial states, and parameters can easily be changed and the different outcomes compared. So, models can be used to identify trends or to estimate uncertainties in forecasts. Different detection, prevention and control strategies can be tested and evaluated.

While the model analysis may require sophisticated analytic or computational methods, mathematical modeling ideally leads to conceptual insight, which can be expressed without elaborate mathematics.

A model is, purposefully, a simplification or abstraction; very often it is an oversimplification or overabstraction. Insight obtained from a model should be checked against empirical evidence and common sense. It can also be checked against insight from other models: how much does the model’s behavior depend on the degree of complexity, on the form of the model equations, on the choice of the parameters? Dealing with a concrete problem, a modeler should work with a whole scale of models starting from one which is as simple as possible to obtain some (hopefully) basic insight and then adding complexity and checking whether the insight is confirmed. Starting with a complex model has the risk that the point will be missed because it is obscured by all the details.

The use of a whole range of models also educates the modeler on how critically qualitative and quantitative results depend on the assumptions one has made. A mathematical modeler should become a guardian keeping him/herself and others from jumping to premature conclusions.

When modeling concrete phenomena, there is typically a dilemma between incorporating enough complexity (or realism) on the one hand and keeping the model tractable on the other. In some cases the modeler feels forced to add a lot of detail to her/his model in order to grasp all the important features and ends up with a huge number of unknown parameters, which may never be known even approximately and cannot be determined by fitting procedures either. Such a mathematical model will be of limited value for quantitative and maybe even qualitative forecasts, but still has the other benefits described above.

Mathematical modeling has its place in all sciences. This book, according to the interests of the author, concerns mathematical models in the biosciences, or rather a very small area within the biosciences, namely population biology. Another restriction is the one to deterministic models (as opposed to stochastic models), which neglect the influence of random events. To some degree one can dispute whether stochastic models are more realistic than deterministic models; there is still the possibility that everything is deterministic, but just incredibly complex. In this case, stochasticity would simply be a certain way to deal with the fact that there are many factors we do not know. Stochastic models are theoretically more satisfying as they count individuals with integer numbers, while deterministic models, usually differential or difference equations, have to allow population sizes that are not integers. (This actually is of no concern if population size is modeled as biomass and not as number of individuals, but the latter is not always appropriate.) While a typical tool of deterministic-model analysis consists of discussing large-time limits, stochastic models take account of the truism that nothing lasts forever and make it possible to analyze the expected time until extinction—a concept that has no counterpart in deterministic models. In many cases, deterministic models can theoretically be justified as approximations of stochastic models for large populations sizes; however, the population size needed to make the approximation good enough may be unrealistically large. Nevertheless, deterministic models have the values which we described above, as long as one keeps their limitations in mind. The latter particularly concerns predictions, which are of very limited use in this uncertain world if no confidence intervals for the predicted phenomena are provided.

Bibliographic Remarks

Other discussions of mathematical modeling can be found in Lin, Segel (1974, 1988), Hethcote, Van Ark (1992), Kooijman (2000), and Kirkilionis et al. (2002). Section 1.1 in Lin and Segel's *On the Nature of Applied Mathematics* more generally speaks about the scope, purpose, and practice of applied mathematics (also in comparison with pure mathematics and theoretical science), while Section 1.6 in Hethcote, Van Ark (1992), *Purposes and limitations of epidemiological modeling*, refers to the modeling of infectious diseases and of the

AIDS epidemic in particular. Their respective remarks, however, easily specialize or generalize to mathematical modeling. A “playful” approach to the role of modeling and mathematics in the sciences can be found in Sigmund (1993, Chapters 1, 3, and 9). The idea that a concrete problem should be addressed by a chain of models has been realized in a textbook by Mesterton-Gibbons (1992), who calls this the layered approach. Section 1.2 in Kooijman (2000) shares the philosophical touch of this chapter; the outlooks are rather similar for modeling itself, but quite different in the meta-modeling aspects. For a discussion of deterministic versus stochastic models see the papers by Nåsell (n.d.) and Section 1.6 in the book by Gurney, Nisbet (1998). Genetic and evolutionary aspects of population biology are not touched on at all in this book, and I refer to the books by Bürger (2000), Charlesworth (1980, 1994), Farkas (2001), and Hofbauer, Sigmund (1988, 1998) as sources for their mathematical modeling and analysis.